MADROÑO

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STUDIES IN NORTH AMERICAN VOLVOCALES. I. THE GENUS GONIUM[1]

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In the course of a field study of *Volvox* in North America, other members of the Volvocales were repeatedly encountered, one of the commonest among them being *Gonium,* which in spring and early summer is often found in rain-water pools similar to those in which *Volvox* may occur. No particular attention was paid to this genus during the journey across America, but later at the University of California time was diverted from the study of *Volvox* to this much simpler member of the Volvocaceae which was appearing in nearly all the soil cultures made in the laboratory as well as in many algal collections made in the neighborhood of Berkeley, California. Since most of the soil-samples used in these cultures were collected in Nebraska and California, where, too, the greater part of the field work was done, the present account is based on material from those two States. The work has continued in South Africa, using soil collected during the American trip some years previously, as well as some from Australia. Obviously the results obtained are by no means exhaustive, and further study would probably add considerably to our knowledge of the *Gonium* flora of North America.

Of the five forms considered here, two have been found only in soil cultures and have not as yet been collected in the field, two others have been so collected and have also appeared in cultures; the fifth, *G. sociale,* was collected once in Berkeley. When possible the algae were isolated and raised in uni-algal cultures either by the soil-and-water method of Pringsheim (1946, p. 13) or in culture solution made according to the recipe given by Juller (1937, p. 61); both single-colony and many-colony inoculations were made, and all forms except *G. sociale* usually proved tolerant of culture conditions so that very rich growths of the various forms could be obtained.

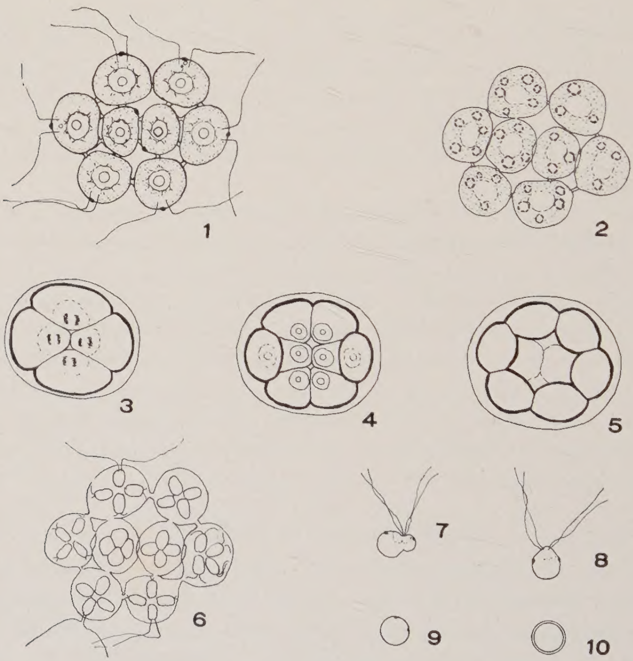
Description of the Species

Gonium octonarium sp. nov. (Lat., octonarium, composed of eight) (figs. 1-15). Species parva, saepe paene sine colore, cellulis octo, sex marginalibus duabus minoribus centralibus, valde regulariter ordinatis: linea transversa duabus centralibus duabus marginalibus formata est, supra et infra duas centrales reliquis quattuor marginalibus positis; centralibus lateraliter paullum compressis, marginalibus omnibus a latere centralibus adiacenti plerumque paullum complanatis; in culturis recentibus cellulae chlorophyllo et pyrenoidibus carnet; in veteribus coenobia pigmentum

[1] The work described here was done during the tenure of Senior Bursaries granted by the Council for Scientific and Industrial Research of South Africa.

viride aliquando habent sed semper pallidissimum, pyrenoidibus tum praesentibus; in reproductione asexuali sex cellulae marginales sese dividunt plerumque prius quam centrales. Coenobium 46–54 $\mu \times$ 38–45 μ; cellulis centralibus 9–12 $\mu \times$ 11–15 μ, cellulis marginalibus 11–14 $\mu \times$ 13–16 μ.

A small species, often nearly colourless, composed of eight cells, six marginal and two smaller central cells, very regularly arranged; the two central cells and two marginal cells forming a transverse row, with the remaining four marginal cells above and below the two central cells; central cells slightly compressed laterally, all the marginal cells usually somewhat flattened on the side adjacent to the central cells; cells in young cultures lacking chlorophyll or pyrenoids, in older cultures the coenobia sometimes containing green pigment but always very pale, pyrenoids then present; in asexual reproduction the six marginal cells usually dividing before the central cells.



FIGS. 1–10. *Gonium octonarium*. FIG. 1. Nearly mature colony, colourless and without pyrenoids, showing attachment between cells, central nucleus with large nucleolus, flagella, eyespots. FIG. 2. Colony from older culture showing pyrenoids surrounding central nucleated region. FIGS. 3–5. Daughter colony formation: *3*, anaphase; *4*, cleavage of third division; *5*, cell division complete, embryo ready to invert. FIGS. 6–10. Sexual reproduction: *6*, sexual colony showing gamete formation; *7*, conjugation; *8*, planozygote; *9*, *10*, zygospore before and after wall formation. Figs. 1, 2, 6 $\times$ 500; all other figures $\times$ 1000.

Habitat and Distribution. In rain-water pools, often those used as drinking pools by cattle grazing on pasture land. Hitherto known only from Nebraska and California; probably widespread but overlooked. Obtained only from soil cultures; not yet collected in the field. Nebraska: rain-water basin, Utica, Seward County; small pond in pasture land, Dinneen's farm, near Exeter, Fillmore County. California: pond in pasture land 4 miles south of Lemon Cove, Tulare County (type locality); vernal pools adjacent to the Santa Fe Grade near Los Baños, Merced County; inundated meadow south of Thornton (19 miles north of Stockton), San Joaquin County; shallow soil in holes in the rock in which rain or snow accumulates, El Moro Rock, Sequoia National Park, Tulare County.

Observations. A very pretty and distinctive little species; when first observed in a soil culture from Utica, Nebraska, it was entirely destitute of chlorophyll and either colourless or faintly flesh-pink, with no sign of pyrenoids (fig. 1); later in the life of the culture it became very pale green. In cultures in which there is not much organic matter it soon develops chlorophyll and pyrenoids but it is typically much paler than other species of *Gonium* which are usually associated with it. When pyrenoids are present several develop in each cell in the cytoplasm around the central nucleus (figs. 2, 12, 13).

The wall of the cell is closely adpressed to the protoplast, and even when treated with methylene blue can only be distinguished as a faint blue line with slight projections at the points of attachment between cells. The mode of attachment is interesting—normally the four cells of the median row are attached to one another at two points, whereas there is usually only one point of attachment between adjacent marginal cells and between the upper and lower two marginal cells and the central cells (figs. 1, 2, 12, 13). Exceptions to the rule are, however, not uncommon. The cells of the median row are closely approximated, the spaces between them and the upper and lower rows being comparatively large. The position of the eyespot in the respective cells and the relation of eyespot, contractile vacuoles, and flagella (more than double body length) are shown in figure 1.

The origin of the median row and its relation to the remaining four cells can easily be traced. After the second division two of the resultant cells widen tangentially, the two alternate cells radially. The third nuclear division, in which the axes of all four spindles are parallel, is immediately followed by cleavage which is radial in the two cells which had widened tangentially thus resulting in the two cells of the upper and lower marginal rows respectively, whereas in the two cells which had widened radially the cleavage is tangential and inclined to the plane of the marginal cells. As a result, the two inner cells, which are rather smaller than the two outer, lie in a plane below that in which the marginal cells all lie (figs. 3–5); the embryo is now a shallow saucer with the central cells at the bottom of the saucer (fig. 15). Inversion follows, which as usual in *Gonium* (cf., Pascher,

1927, p. 414), consists of a reversal of the curvature of the young saucer-shaped embryo, thus bringing the two central cells slightly forward of the marginal cells to form the anterior pole of the colony as it progresses through the water. It is of interest to find that in daughter-colony formation these two central cells lag behind the others and may still be undivided when all the marginal cells have either completed or nearly completed embryo formation (fig. 14). Thus there is more than a suggestion of somatic differentiation.

Throughout the process of cell-division and reorientation the embryo is attached to the parental flagella and the colony remains motile. Pascher states that the developing embryo becomes free from the flagella prior to inversion, but this is not normally the case in the forms studied by the writer; when it does occur it is probably an abnormality.

Sexual reproduction was observed once in the early hours of the morning (1 a.m. onwards) in a culture of soil from Utica. The culture was very vigorous with many young colonies in process of development, but it presented a strikingly different appearance from those usually seen, as many small colonies showed groups of four cells in each constituent cell. These were arranged as if to form daughter colonies, but instead of escaping as such, the cells of each group proceeded to separate, escape from the parental cell-membrane, and become gametes. In all the cases of conjugation observed, the gametes were unequal in size. The difference in size may be attributable to variation in size of the parent cell or perhaps to a difference in the number of gametes formed in each, although only four-celled groups were seen. In hanging drops in deep depression slides kept in a moist chamber, liberation and copulation of gametes continued for some hours, while colonies remained active for several days. The planozygotes were actively motile for some time, usually but not always settling down in less than an hour after completion of conjugation, then withdrawing their flagella and forming small rounded resting spores (4–5 μ when first formed, enlarging to 6–8 μ on completion of wall formation). At first the zygospore was almost colourless, but later became pale golden brown with a thin smooth wall. In soil cultures under favorable conditions, young colonies may appear within 24 hours after addition of water, or their

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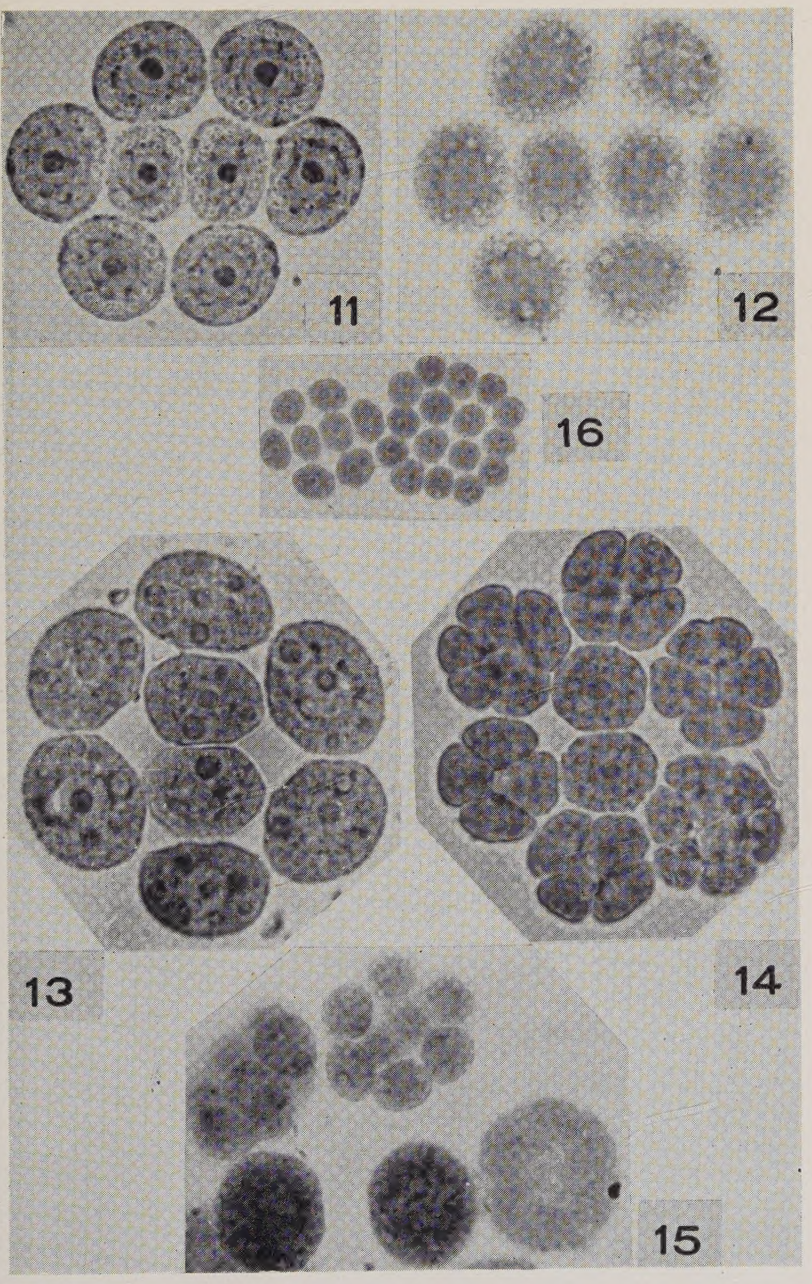
EXPLANATION OF FIGURES

FIGS. 11–15. *Gonium octonarium*. FIG. 11. Nearly mature colony, colourless, without pyrenoids (Santa Fe Grade culture), stained with aceto-carmine to show nucleolus. × 1000. FIG. 12. Nearly mature colony from older culture (Utica culture), showing many small pyrenoids. × 1000. FIG. 13. Large green colony with many pyrenoids (Lemon Cove culture), showing mode of attachment between cells. × 960. FIG. 14. Mature colony (Santa Fe Grade culture), showing central cells undivided, marginal cells forming daughter colonies: three 4–celled, two preparing for last division and one with third cleavage nearly complete. × 1000. FIG. 15. Part of mature colony (Utica culture), showing two central and one marginal cell of central row undivided and two cells of upper row with daughter colonies ready to invert. × 1500. FIG. 16. Nearly mature colony of *G. octonarium* and young colony of *G. multicoccum*, stained with aceto-carmine (Lemon Cove culture). × 440.



FIGS. 11–15. *Gonium octonarium.*

appearance may be delayed to a later stage in the life of the culture; temperature appears to be the chief determining factor. The resting spores may retain their viability for years, in some cases the soil used in the cultures having been collected over four years previously.

This species responds well to cultural conditions. Rich cultures were obtained from both single- and many-colony inoculations by using the soil-and-water technique, usually in Pyrex test tubes. Such cultures have been maintained for weeks, and in them development of pigment accompanied by formation of pyrenoids is usually much more marked than in the original soil cultures.

Gonium pectorale Müller (1773). This cosmopolitan, typically 16-celled species is much the best known and is probably the commonest of all the colonial Volvocales. It is so frequently met that one is inclined to pass it by without further examination, but probably it includes many forms, some of which are certainly worthy of varietal rank; one such is described here. The typical form (var. *pectorale*) was also observed and appears to be widespread in North America.

Gonium pectorale Müller var. **pectorale** (fig. 17). Colonies of this variety are characteristically bright green. In addition to the 16-celled colonies, 8- and even 4-celled individuals may occur, or according to Pascher (1927, p. 412, footnote), occasionally even colonies of between 16 and 32 cells. The coenobium takes the form of a nearly square plate, not quite flat but usually bent back slightly along the two diagonals. Mature cells are nearly spherical with a single large basal pyrenoid. Pascher gives 90 μ as the limit of size, with the cells 10 μ wide by 14 μ long, but the North American material may be considerably larger, well over 100 μ in diameter with cells 18 $\mu \times$ 20 μ. In other respects it agrees reasonably well with the descriptions of European material.

As the cell matures, the single pyrenoid increases in size almost filling the base of the massive bowl-shaped chloroplast so that the floor of the colourless nucleated region is pushed up, thus compressing the nucleus which consequently becomes spheroidal. Hence, though in polar view the colourless nucleated region is circular in outline, viewed from the side it appears elliptical (fig. 17).

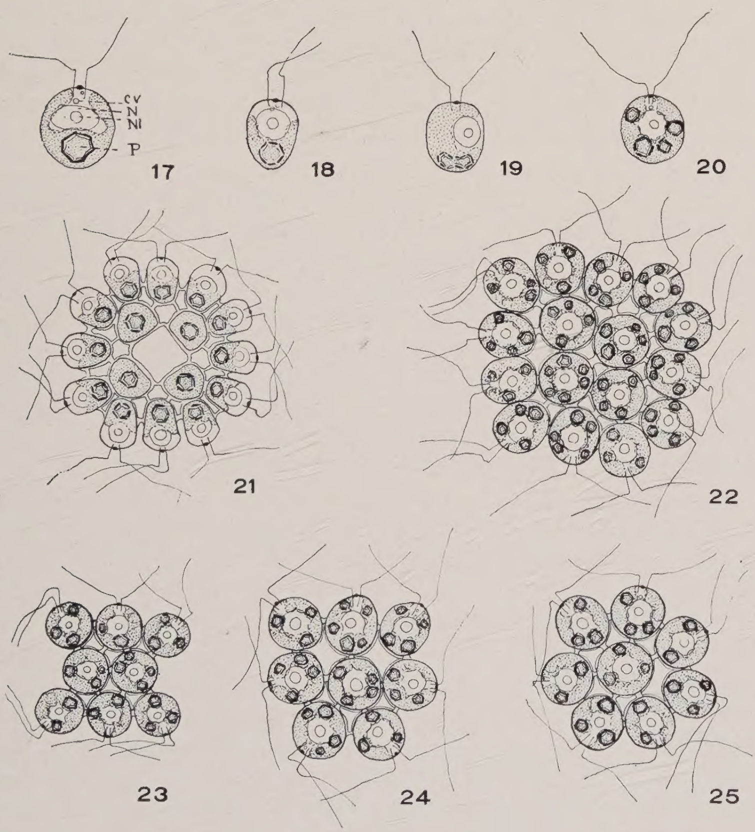
Habitat and Distribution. Temporary fresh water pools, ponds in pasture land, lakes, etc. Probably widespread in North America. Collected in small lakes in Wisconsin; rain-water pools in Nebraska; in California collected near Walnut Grove, in Jackson Slough near Isleton (Sacramento County), and in the neighborhood of Stockton (San Joaquin County). Cultures of the latter provided most of the material used in the cytological investigation of this species (Cave and Pocock, 1951). Also in cultures of soil from Nebraska (Utica, Seward County) and California (Lemon Cove, Tulare County; Santa Fe Grade, Merced County).

Observations. Daughter colony formation was never observed to occur until the colonies had reached a large size; there was no indication of cell

differentiation within the colony as regards commencement of division—sometimes the cells of a colony began to divide more or less simultaneously, sometimes one or more of the central cells dividing before the marginal, but there was no definite order, and there appears to be a marked absence of synchronization between the cells in respect to division. Behaviour of different cultures is considered later.

Gonium pectorale var. **praecox** var. nov. (figs. 18, 19, 21). Coenobium adultum parvum, cellulis plerumque 16, ovatis, singulis unaquaque pyrenoidibus. Coenobium 50–64 $\mu \times$ 54–68 μ; cellulis 10–12 $\mu \times$ 13–14 μ.

Mature colony comparatively small, usually rather pale green and slightly oblong in shape; cells somewhat elongated, ovoid in side view



Figs. 17–20. Mature cells. *17, Gonium pectorale* var. *pectorale*; (*N*, nucleus; *Nl*, nucleolus; *CV*, contractile vacuole; *P*, pyrenoid); *18, 19, G. pectorale* var. *praecox; 19,* showing reorientation of parts prior to division; *20, G. multicoccum.* Figs. 21–25. Nearly mature colonies: *21, G. pectorale* var. *praecox;* figs. *22–25, G. multicoccum; 22,* showing slightly rhomboidal 16-celled colony; *23–25,* 8-celled colonies showing various types of cell arrangement. All figs. ca. $\times$ 500.

with apex usually wider than the base in which the single large pyrenoid lies, colourless apical region containing the spherical nucleus larger and more conspicuous than in var. *pectorale* (figs. 18, 21); in young colonies the central space often large so that the central cells appear to be pushed into the corners; bases of the two corner cells of the margin consequently slightly angular.

Habitat and Distribution. Fresh water ponds and pools. Obtained in a culture of soil from Lemon Cove, Tulare County, California (type locality) associated with *G. octonarium* and the following species. Probably future study will show that it is not uncommon.

Observations. Daughter colony formation may begin in quite small colonies whence the varietal name since precocious development is one of the chief distinguishing features of this variety. For example, in a colony measuring 50 μ × 54 μ all the marginal cells had already divided once or twice while the still undivided central cells measured 10 μ × 13 μ, and even smaller colonies may have begun to divide. Division may start in either marginal or central cells or more or less simultaneously in all. No indication of somatic differentiation was observed.

Nuclear division is preceded by a shift in the parts of the protoplast, the colourless apex moving to one side while the nucleus itself migrates toward the surface of the cell (fig. 19). This change in cell polarity takes place in the same direction in all the marginal cells, while a similar sequence, not necessarily in the same direction, is seen in the four central cells. The regularity of this change in position of the constituents of the protolast is most striking. At the same time the pyrenoid begins to widen and as nuclear division takes place the pyrenoid also divides. Successive nuclear divisions are accompanied by division of the pyrenoids, and eventually each daughter cell receives a single small pyrenoid.

Gonium multicoccum sp. nov. (figs. 20, 22-25, 26-30). Coenobium adultum magnum, cellulis 8, 16 aut 32, subglobosis, multis unaquaque pyrenoidibus. Coenobium (cellulis 16) 60–76 $\mu \times$ 62–78μ; cellulis 13–18 μ × 16–19 μ.

Adult coenobium large, of 8, 16, or 32 cells; cells more or less globose, with a number of pyrenoids of varying sizes almost surrounding the central spherical nucleus. Cells of the colony evenly spaced, separated by comparatively small spaces; no large central aperture.

Habitat and Distribution. Ponds, inundated meadow land, fresh-water basins, etc. UNITED STATES. Nebraska: fresh-water basin, Utica, Seward County. California: inundated meadow south of Thornton (19 miles north of Stockton), San Joaquin County; pond 4 miles south of Lemon Cove, Tulare County (type locality). Also in cultures of soil from all three localities. AUSTRALIA. New South Wales: Flooded meadow, Woodlawn Road near Lismore (soil culture).

Observations. The cells of the colony are more closely apposed than in *G. pectorale;* young colonies may show hardly any spaces between the

cells. As development proceeds the cells separate slightly but evenly, and there is a marked absence of the large central aperture which characterizes the varieties of *G. pectorale* (figs. 26–29). Two of the central cells are normally joined across the comparatively small central space (figs. 22, 28).

When first formed the cells of the young colony each contain a single basal pyrenoid, but while still quite small the pyrenoids begin to increase in number, first one and then another appearing until there may be 6 or 8, or in well grown colonies as many as 10 to 12 in each cell. For example, in a colony 29 $\mu \times 35$ μ with cells only 6 μ in diameter, most of the cells already contained two pyrenoids; another still immature colony 65 μ wide with cells 15 μ in diameter had 5 or 6 pyrenoids in each cell. Apparently the secondary pyrenoids are formed *de novo* and not by division of pre-existing pyrenoids; they are of varying sizes, the primary pyrenoid usually larger than those formed subsequently. In contrast to *G. pectorale* var. *praecox,* the colourless apical area is reduced to a minimum and is barely discernible in surface view of the colony (figs. 20, 22–24).

In addition to the 16-celled colonies, 32-celled colonies may be fairly numerous in vigorous cultures, while on the other hand there is always a large proportion of 8-celled colonies. In colonies of the latter type the arrangement of the cells is strikingly different from that in *G. octonarium.* The commonest arrangement is three rows—two of three cells each with a central row of two cells—basically resulting from the arrangement of the cells at the 8-celled stage of division when there are four central cells in the form of a cross with four marginal cells in the angles of the arms of the cross (figs. 23, 29, 30). In other instances the rows are in the order of 3-3-2 cells (fig. 24), whereas in yet others as development proceeds the cells become further displaced and more or less rounded colonies result, with a single central cell surrounded by seven marginal cells (fig. 25). A close examination of the mode of attachment between cells may indicate how these various arrangements have arisen from the initial 8-celled pattern. It must be clearly understood that all these forms are due, not to fragmentation of an originally 16-celled colony but to the fact that the parent cell has divided three times only instead of four.

The 32-celled colonies are, however, the most striking feature of this species. They are beautifully symmetrical, octagonal in outline but not quite isodiametric—two sides parallel to the longer diameter consist of four cells, whereas the remaining six sides are all 3-celled, the corner cell in each instance being common to two adjacent sides. The arrangement of the cells is 18 peripheral, 4 central and 10 intermediate (figs. 26, 27) When first observed in early summer of 1949 in a rich collection of algae from an inundated meadow south of Thornton, it was thought that the 32-celled plates might represent a species distinct from the 8- and 16-celled colonies with which they were associated. Single colony cultures were

established using complete or nearly complete 32-celled individuals for inoculation, but in every case the resultant culture was composed of 8- and 16-celled colonies; later cultures raised from 16-celled inoculations sometimes produced 32-celled offspring. Obviously therefore the 32-, 16- and 8-celled colonies all belong to the same species, which, unlike *G. pectorale*, is characterized by the presence of many pyrenoids in each cell.

When fully mature the constituent cells are as large as in *G. pectorale* var. *pectorale*, but since the intervening spaces are smaller the colonies are, as a rule, proportionately smaller. The dimensions given above are all for 16-celled coenobia; 32-celled individuals naturally reach a much larger size. The one shown in Figure 27, though far from mature, with cells still only 12 $\mu \times$ 13 μ and containing only 3 or 4 pyrenoids, already measured 88 $\mu \times$ 96 μ.

In 1953 numerous cultures of soil from Lemon Cove, California, were made in South Africa at Grahamstown; several of these produced beautiful growths rich in 32-celled colonies, and it was possible to study the development and behaviour of the various types of colonies. Taking the 16-celled coenobium as the norm, it was interesting to find that on the whole the 8-celled form was the most abundant in young cultures, was the most stable and tended to reach maturity earliest, whereas 32-celled individuals made their appearance later in the life of the culture, developed more slowly than either the 8- or 16-celled colonies with which they were associated, full maturity culminating in the formation of daughter colonies being reached later than in either of the other forms; further, 32-celled colonies tend to fragment more readily.

Sexual reproduction has not as yet been observed in this species.

Gonium sociale (Dujardin) Warming (1876). This 4-celled species was collected in early summer by Dr. Lee Bonar in the fishpond in his garden at Berkeley. Unfortunately, little time could be spared for it and the few attempts made to get it established in culture failed, although it continued active for some weeks in the water in which it had been collected. Addition of culture solution to the original water did not noticeably stimulate growth.

The colonies were small and pale in colour and were apparently growing in water containing far less organic matter than in most of the soil cultures studied. Two-celled colonies sometimes occurred, but never colonies of

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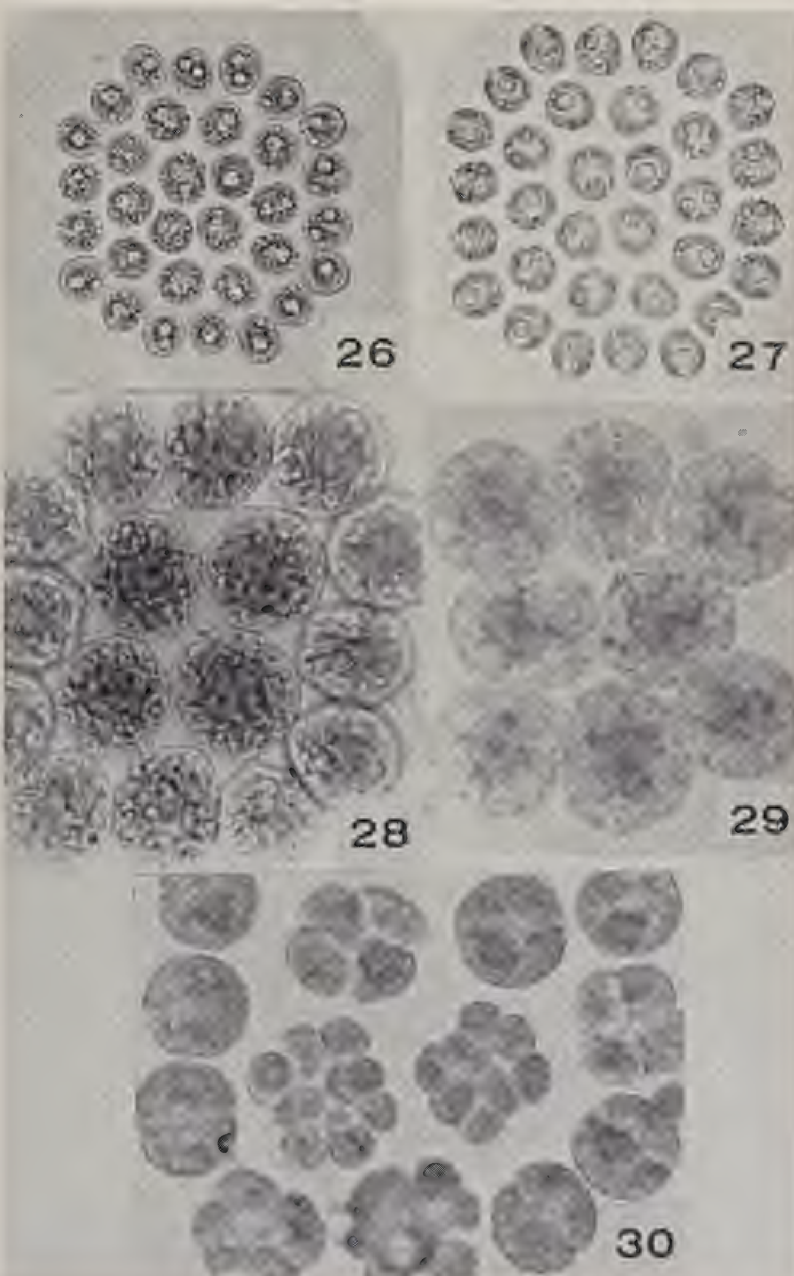
Explanation of Figures

Figs. 26–30. *Gonium multicoccum*. Figs. 26, 27. 32-celled colonies fixed in osmic acid vapour (Thornton Meadow culture): *26*, showing flagella and pyrenoids, $\times$ 430; *27*, showing at a slightly lower focus the marginal cells with clear apical area, eye-spots, etc., $\times$ 490. Fig. 28. Nearly mature 16-celled colony with the central cells in focus to show absence of central aperture and attachment between the cells (Lemon Cove culture). $\times$ 960. Fig. 29. 8-celled colony from same culture stained with aceto-carmine. $\times$ 960. Fig. 30. Part of 16-celled colony showing undivided cells and developing embryos in 2-, 4- and 8-celled stages. $\times$ 960.



FIGS. 26–30. *Gonium multicoccum*.

more than four cells. Colonies of this species were quite easily distinguishable from the 4-celled colonies which may occur in any other species of *Gonium*. The species is apparently widespread but by no means common, and little is known about its life-cycle and behaviour. It has not appeared in any cultures of soil from North America nor has it yet been reported from South Africa.

Observations on Cultures

As the first rich cultures of *Gonium pectorale* made in the laboratory at Berkeley approached maturity, they were closely watched for dividing cells, but no matter what the hour of the day none could be found although many young colonies were always present. Observation was therefore started at night, and at once divisions were found; as night advanced, the number of colonies showing stages in division increased. The first evening division apparently started between 7 and 8 o'clock and increased rapidly until about 9 p.m. when an optimum was reached and nearly all the larger colonies showed stages in division. This period of intense activity lasted for a time; then the number of dividing colonies gradually decreased until at about 10:30 p.m. no more divisions could be found. Observations were repeated on several succeeding nights with comparable results except that there was a gradual shift in the time of successive stages to a slightly later hour.

These observations led to the conclusion that in *Gonium* nuclear division, followed immediately by cell cleavage, was a nocturnal phenomenon. This conclusion, however, proved to be unwarranted for a few weeks later another culture was found to be dividing in the early afternoon, while in yet a third instance division took place in the morning. Quite recently, in a soil culture in which several forms of *Gonium* were flourishing, *G. octonarium* was dividing actively at night while *G. multicoccum* showed hardly any stages in division but was found to be dividing freely in the early forenoon.

There is therefore no stereotyped rule for the time at which division occurs in *Gonium*. All that can be said with certainty is that in any given population there appears to be an optimum time for nuclear division, but that this optimum may vary considerably in different populations or for different forms growing side by side in the same culture. It is difficult to estimate what factors may be operative; undoubtedly external factors play an important role in determining the behaviour of a culture, but obviously they are not alone responsible for variations in behaviour in this respect. Response to external conditions appears to be modified by some inherent factor or factors in any given strain and in any culture. Further, there appears to be a rhythm which is not strictly diurnal since there may be a progressive shift in the time of optimum division. Extended study of behaviour in numerous cultures under varying conditions might do much to solve this as well as many other problems in the life cycle of *Gonium* and

other green algae. *Gonium* would appear to be a particularly favorable subject for such a study.

Discussion

In a cosmopolitan and moreover highly variable alga such as *Gonium* one hesitates to create new varieties or species; only when characteristic features, whether of structure or behaviour, prove constant and readily recognizable is such a course justifiable. The question then arises as to whether such variants constitute new species, or whether they should be regarded as varieties or merely forms of existing species. In the case of *G. octonarium* described here as new, from its first recognition there could be no doubt that it was a distinct, undescribed species. No other species of *Gonium* shows such constancy of number and arrangement of cells, combined with such individuality of cell-structure. But the other two taxa, both usually 16-celled with cell arrangement essentially similar to the cosmopolitan *G. pectorale* var. *pectorale,* could easily be passed over as that species. This is particularly true of the small form here named *G. pectorale* var. *praecox* in which there is a single basal pyrenoid. At first it was regarded as merely a form of *G. pectorale* var. *pectorale,* but there are distinct differences, not only in the shape of the cells with the conspicuous apical region but also in their arrangement in the colony, in the precocious maturation and in the regularity of the shift in the polarity of the cell prior to division. These features are regarded as justifying varietal rank. In *G. multicoccum,* the differences are even more marked; here, although the shape of the cell is similar, its structure (with numerous pyrenoids scattered through the cytoplasm around the spherical nucleus and the small colourless apical region) and the compact arrangement of the cells in the colony without a large central space distinguish it from *G. pectorale* even when only the 16-celled form is considered. The numerous 8-celled, and still more the regular 32-celled colonies, further distinguish it; taken together these characters are regarded as sufficiently distinct to justify the view that it constitutes a separate species.

Until comparatively recently the species of *Gonium* recognized as distinct have all been either 4- or 16-celled, but in 1942 Prescott described a 32-celled species, *G. discoideum* ["constantesque 32 (raro 16) singulis cellulis"] from Louisiana. This species differs from *G. multicoccum* from California in the shape of the colony which is rounded in outline instead of octagonal, and in the form of the cells which are irregularly pyriform with two basal pyrenoids. The arrangement of the cells—4 central surrounded by two series of 10 and 18 respectively—is the same in both of these species. But in the California material (Thornton Meadow and Lemon Cove collections) 32-celled colonies were comparatively few and 16- and 8-celled colonies far more numerous. Furthermore, single colony cultures clearly demonstrated that the 32-celled colonies did not represent a species distinct from the 8- and 16-celled colonies with which they were associated.

Crow (1927), in his account of abnormal forms of *Gonium* in Great Britain reports the occurrence of 8-, 4- and 2-celled colonies in *G. pectorale,* and points out that such colonies may originate either by a reduction in the number of cells formed by division of the parent cell or by fragmentation of normal 16-celled colonies. He adds: "the eight-celled form does not appear to be represented by a distinct species," and discusses possible reasons for this absence, concluding that a "central aperture" in the colony is necessary due to the way the organism swims. Hence, the discovery of an 8-celled species has special interest since it fills a gap in the series of types of colony structure within the genus. Crow's explanation for the absence of such a species obviously becomes unnecessary. He also mentions the occasional occurrence of ring-shaped colonies formed by the dropping out of the central cells in normal 16-celled colonies. Similar forms have been observed in the course of this work, but apparently the circular 8-celled colonies described above in *G. multicoccum* have not been noted in typical *G. pectorale*. Possibly they are peculiar to *G. multicoccum* wherein other types of 8-celled colonies are also formed in unusually large numbers.

The number of pyrenoids in a cell may sometimes be of diagnostic value as a specific character, as in the case of *G. multicoccum,* but since in many algae the number varies during the life cycle, this feature must always be used with caution. In some algae the pyrenoids increase in number prior to cell division, in others they may disappear entirely. In *Gonium* there seems to be considerable variation in pyrenoid behaviour; in *G. pectorale* var. *pectorale,* pyrenoid behaviour has not been studied, but in the variety *praecox* division of the pyrenoid accompanying nuclear division seems to be the rule, whereas in *G. multicoccum* numerous pyrenoids are formed *de novo* during the maturation of the cell. The disappearance of the pyrenoids during cell division, a characteristic of many algae, does not seem to occur in *Gonium*. These statements are, however, made with some reserve and more work is needed to elucidate fully pyrenoid behaviour in the genus—possibly both methods of pyrenoid formation will be found to occur in any one form, one or the other predominating.

A change in the polarity of the cell prior to division is a phenomenon which may be observed in various members of the Volvocaceae including *Volvox* (Pocock 1933, p. 587); it is fairly general in *Gonium* but nowhere has such regularity been observed as in *G. pectorale* var. *praecox*. Exceptional cases may occur in which the regular "follow my leader" fashion fails and the nuclei of two successive cells come to lie on adjacent sides, but this is rare and usually the marginal cells and consequently the daughter colonies formed by them all face the same way, the central cells showing a similar mutual sequence. Later in development the embryo colonies tend to swing around until they lie in the plane of the parent colony. Possibly the change in polarity of the cell is directly connected with the retention of motility throughout daughter-colony formation.

Since conflicting accounts have been given as to the way in which *Gonium* moves, it seems advisable to give a brief description of movement as observed during this work. As the colony is normally slightly convex, the central cells constitute the "anterior pole" of the coenobium; movement is two-fold: rotation on an axis perpendicular to the colony through the center and a forward progression along the line of this axis. The normal position of the plate during movement is thus on edge, while at rest the tendency is for it to present a surface view. There is never any indication of "progression by a series of somersaults" as described by some workers, but the rotary movement may be slightly jerky.

The beginning of somatic differentiation seen in *Gonium octonarium* is of particular interest since no such differentiation has been noted in any other species. Much still remains to be elucidated as to sexual reproduction, in particular, whether the presence of plus and minus strains recorded by Schreiber (1925) in *G. pectorale* are general for all taxa and whether or not all are dioecious. Apparently sexual reproduction is seldom observed, but possibly this may be because the process is a nocturnal phenomenon rather than a rare one. The longevity of the resting spores is probably even more pronounced than has been shown in the course of this work.

Summary

Gonium collected in the field has been supplemented by material obtained from cultures of soil collected mainly in Nebraska and California.

Five distinct forms of *Gonium* have been studied of which two are described as new species—*G. octonarium* (8-celled) and *G. multicoccum* (8-, 16- and 32-celled)—and one as a new variety—*G. pectorale* var. *praecox;* the two remaining forms are *G. pectorale* var. *pectorale* (normally 16-celled, as in var. *praecox*) and the 4-celled *G. sociale.*

The new species and variety are described and observations on the occurrence, life cycle, behaviour and results of cultures of the various forms are recorded.

The discussion deals with taxonomic relationships within the genus; the diagnostic value of pyrenoids and their number and behaviour; change in polarity within the cell prior to division; movement of the colony, and incipient somatic differentiation as seen in *G. octonarium.*

Acknowledgments

My grateful thanks are due to the Faculty of the Department of Botany, University of California, Berkeley, where the work was begun, and especially to the Chairman of the Department, Dr. Lee Bonar, who also supplied me with the material of *Gonium sociale;* to Professor Twyman of the Botany Department of Rhodes University where it was continued; to Dr. Johannes Proskauer, Dr. Isabella Abbott, and Dr. Mary L. Bowerman, all of the University of California; and to Dr. Walter Kiener, Biologist of the Nebraska Game, Forestation and Parks Commission, for material and soil samples; to my brother, Professor L. G. Pocock of Can-

terbury College, University of New Zealand, and to Mr. S. Whiteley of Rhodes University for the Latin descriptions; and finally to Dr. G. F. Papenfuss and Dr. Marion S. Cave for so kindly reading the manuscript, seeing it through the press, and for much helpful advice.

Grahamstown, South Africa

Literature Cited

Cave, Marion S. and Mary A. Pocock. 1951. Karyological studies in the Volvocaceae. Am. Jour. Bot. 38:800–811.

Crow, W. B. 1927. Abnormal forms of Gonium. Ann. Mag. Nat. Hist., Ser. 9, 19: 593–601.

Fritsch, F. E. 1935. The structure and reproduction of the algae. Vol. 1. Cambridge. 791 pp.

Juller, E. 1937. Der Generations- und Phasenwechsel bei Stigeoclonium subspinosum. Archiv Protistenk. 89:55–93.

Müller, O. F. 1773. Vermium terrestrium et fluviatilium, seu animalium infusiorum, helminthicorum et testaceorum, . . . Vol. 1, pt. 1 [32]+ 135 pp. Copenhagen and Leipzig: Heineck & Faber.

Pascher, A. 1927. Die Süsswasserflora Deutschlands, Österreichs und der Schweiz, Vol. 4, Jena. 506 pp.

Pocock, Mary A. 1933. Volvox in South Africa. Ann. So. Afr. Mus. 16:523–646.

Prescott, G. W. 1942. The algae of Louisiana, with descriptions of some new forms and notes on distribution. Trans. Am. Micr. Soc. 61:109–119.

Pringsheim, E. G. 1946. Pure cultures of algae, their preparation and maintenance. Cambridge. 119 pp.

Schreiber, E. 1925. Zur Kenntnis der Physiologie u. Sexualität höherer Volvocales. Zeitschr. Bot. 17:336–376.

Smith, G. M. 1950. The fresh-water algae of the United States. 2d ed. New York. 719 pp.

Warming, E. 1876–1877. Om en fircellet Gonium (Dujardin's Tetramonas socialis ?). Bot. Tidsskr. Raekke 3, 1:69–83, pl. 1.

FLORA OF THE CRESTED BUTTE QUADRANGLE, COLORADO

Jean H. Langenheim

Although the flora of the eastern slope of the Colorado Rockies has been studied in considerable detail, the western slope has received little attention. Several general surveys which include incomplete floral lists have been published, the most complete being Brandegee's (1876), which was intended to be a supplement for southwestern Colorado to Porter and Coulter's "Synopsis of the Flora of Colorado" (1874). Charles F. Baker also published a very incomplete list for the La Plata Mountains in 1898. Names of plants are mentioned in several vegetational surveys of the state (Robbins, 1910; Cary, 1911), and Schmoll (1935) discussed the vegetation of the Chimney Rock Area, Archuleta County. However, there are no truly definitive lists for local areas other than that by Graham (1937) for the Colorado portion of the Uinta Basin.

The following floristic list was prepared in conjunction with a detailed ecological study in the Crested Butte Quadrangle, and represents collections made to document that study. It is prepared for publication previous to the ecological study at the request of several workers who will find it useful to their research in this area. Voucher specimens are in the herbaria at the University of Colorado and the University of Minnesota. Since the rarer species were deemed to be more useful to workers at the University of Colorado, in many instances the only collections of these are at that institution. Large but incomplete collections are in the herbaria at the Colorado A. & M. College, State University of Iowa, and the University of California at Berkeley. I wish to acknowledge the assistance of W. A. Weber, University of Colorado, in verifying or determining the collection in general. The majority of the Compositae, Gramineae, and Cyperaceae were submitted to H. D. Harrington, Colorado A. & M. College. I am also grateful to the following people for assistance in their special groups: C. R. Ball, *Salix;* Lyman Benson, *Ranunculus;* Bernard Boivin, *Thalictrum;* Lincoln Constance, *Umbelliferae* and *Hydrophyllaceae;* G. J. Goodman, *Eriogonum;* F. J. Hermann, *Juncus;* C. L. Hitchcock, *Draba* and *Lathyrus;* D. D. Keck, *Penstemon;* G. B. Ownbey, *Corydalis;* C. L. Porter, *Astragalus* and *Oxytropis;* C. O. Rosendahl, *Saxifragaceae;* E. T. Wherry, *Polemoniaceae;* Robert E. Woodson, *Asclepias.*

The Crested Butte Quadrangle is located in west-central Colorado on the southwest flank of the Elk Range. It is about 35 miles north of Gunnison and 25 miles southwest of Aspen in Gunnison County (fig. 1). The altitude ranges from 8,000 to 13,500 feet. Many types of bedrock occur here although ninety percent is sedimentary rock; the remainder consists primarily of igneous intrusives. The topography is rugged, being in an early mature stage of the erosion cycle modified by glaciation. Climatic conditions are diverse. The only weather station in the area is located at Crested Butte, 8,867 feet, where an average annual rainfall of 28 inches is reported (U. S. Dept. of Commerce, 1952), but weather bureau estimates are as high as 50 inches in portions of the area. There are two maxima of precipitation: from July to September, and during January. The heavy accumulation of winter snow supplies a persistent source of moisture throughout the summer at high elevations. At Crested Butte the mean temperature for July is 56.8° F. and for January, 13.6° F.; the absolute maximum temperature on record is 91° F. and the absolute minimum, − 42° F. (U. S. Dept. of Agric. Yearbook, 1941). Although the temperature extremes at higher elevations are unknown, it is significant that freezing temperatures occur at irregular intervals throughout the growing season.

The vegetation of this area has been disturbed little by the influence of man since the establishment of the Gunnison National Forest in 1909. However, despite a controlled program of grazing which has prevented widespread erosion, the composition of the grassland and meadow com-

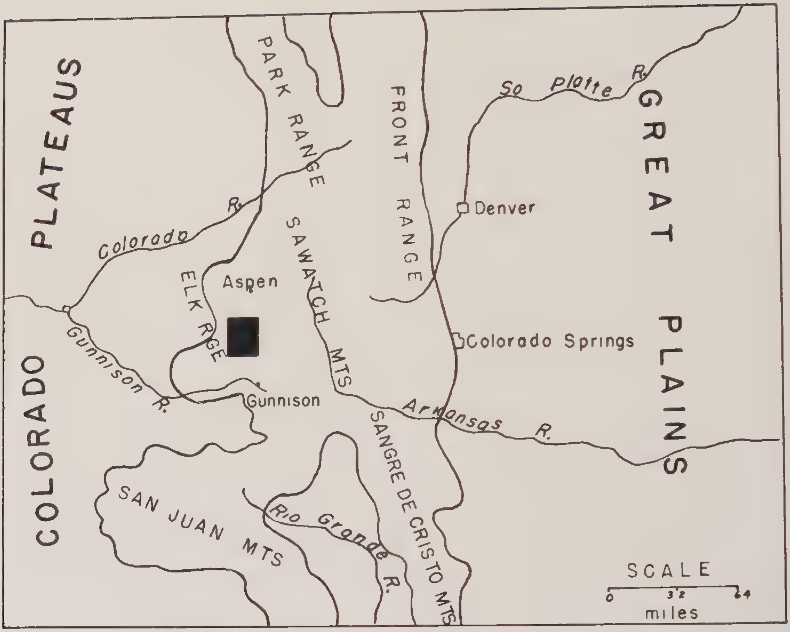


FIG. 1. Index map of Colorado showing location of Crested Butte Quadrangle.

munities has been altered somewhat. A fire history is evident as having occurred between 1880 and 1900, thus coinciding with the peak of mining activity. From this brief discussion, it is evident that the area is one of highly diverse environmental conditions which could be expected to select a rich flora.

The percentages of species representing different floristic elements, as recognized by W. A. Weber (personal communication), are shown in Figure 2. Although the area of the Crested Butte Quadrangle is located on the border of the Colorado Plateau, it is still a part of the Rocky Mountain system. Thus it is not surprising to find that a majority of the species at the elevation of the study area have Rocky Mountain affinities. Further analysis of this Rocky Mountain element shows that the highest percentage of species is either widespread throughout the Rockies or occurs primarily within the Central Rockies; few have Northern Rocky affinities. Species with circumboreal affinities or with distributions widespread over western North America are also common. There is a relatively small representation of species with Great Basin-Colorado Plateau affinities, but observations at lower elevations in the adjacent Gunnison River Valley indicate, as one would expect, a higher representation of species with these relationships.

The flora is organizable into five vegetational zones: sagebrush, aspen, spruce-fir, upland herb, and alpine. The sagebrush zone characterizes the

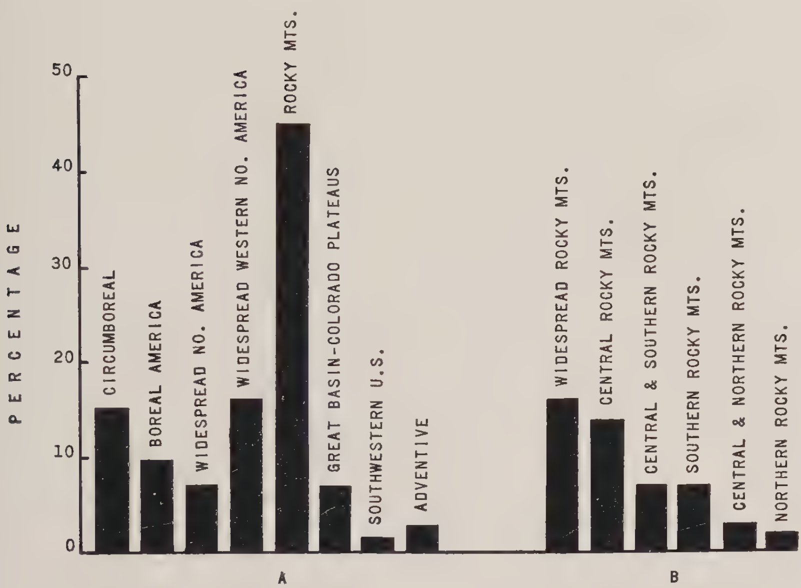


FIG. 2. Floristic relationships of species in the Crested Butte area: A. Percentages of species representing floristic elements recognized by W. A. Weber. B. Analysis of the species in the Rocky Mountain element (see A) into component elements.

8,500-9,500 altitudinal range in the quadrangle and continues downward to approximately 7,500 feet in the adjacent Gunnison River Valley. It seldom occurs above 10,000 feet, but has been observed in patches near timberline. *Artemisia tridentata* is the dominant; other common shrubs are *Chrysothamnus viscidiflorus* and *C. parryi*. *Festuca thurberi* is the most prominent grass, and characteristic forbs are *Achillea lanulosa*, *Eriogonum neglectum*, *Vicia americana*, *Arenaria congesta*, *Erigeron speciosus*, *Lathyrus leucanthus*, and *Potentilla pulcherrima*.

The aspen zone ranges from 8,500 to approximately 11,200 feet. Between 9,500 and 10,500 feet it forms a distinct altitudinal belt, occurring as a continuous open forest below the spruce-fir zone or as groves scattered through the *Festuca thurberi* grassland. *Populus tremuloides* is the dominant. The most common forbs in the mature undergrowth are *Thalictrum fendleri*, *Ligusticum porteri*, *Vicia americana*, and *Erigeron elatior*. *Bromus ciliatus* is the most frequent grass.

The Engelmann spruce-subalpine fir zone is the most extensive one in the Crested Butte area, occurring from 8,500 feet along streamsites to 12,500 feet as patches of *Krummholz*. It is altitudinally well defined, however, only from approximately 10,500 to 11,500 feet. *Picea engelmannii* and *Abies lasiocarpa* are the only tree dominants. A tall shrub layer is composed primarily of *Ribes cereum* and *R. wolfii*. *Vaccinium myrtillus* and *V. caespitosum* make up a low shrub layer which dominates the forest

floor. *Pedicularis racemosa, Arnica cordifolia, Fragaria ovalis,* and *Polemonium delicatum* are the most frequent herbs. Lodgepole pine, aspen, and *Festuca thurberi* with characteristic associates replace burned spruce-fir forest. Replacement has been most extensive by the grassland in this area.

The upland herb zone is most prevalent from approximately 11,500 to 12,500 feet, but also is characteristic of non-forested areas as low as 10,500 feet. This zone consists of a luxuriant assemblage of grasses, sedges, and showy forbs. The most common forbs are *Senecio crassulus, Ligusticum porteri, Lupinus parviflorus, Delphinium barbeyi, Polygonum bistortoides,* and *Helianthella quinquenervis. Carex ebenea* and *C. chalceolepis* are the most common sedges, with *Phleum alpinum, Poa alpina, P. arctica,* and *Trisetum spicatum* the most important grasses.

The alpine zone is best developed between 12,500 and 13,500 feet, although alpine assemblages interfinger with the upland herb zone as low as 12,000 feet. A well-defined population pattern could not be discerned in this altitudinal range. Characteristic groups of species occur on fell fields, boulder fields, on talus, and along streamsides and snowbanks, but dominance varies widely from stand to stand. Arêtes on which fell fields predominate provide most of the area available to alpine species here. This habitat is relatively barren with only scattered herbaceous growth. *Hymenoxys grandiflora, Artemisia scopulorum, Oxytropis deflexa, Erigeron pinnatisectus, Polemonium viscosum,* and *Silene acaulis* are the most frequent forbs. Patches of sedges with some included grasses occur locally. *Kobresia bellardii, Carex elynoides,* and *C. hepburnii* comprise the prominent sedges. The common grasses are *Poa alpina, Trisetum spicatum, Festuca ovina* var. *brachyphylla,* and *Agropyron trachycaulum.*

An extensive bunch grassland dominated by *Festuca thurberi* occurs within the matrix of all zones from 8,500 to 12,500 feet, being most prevalent on deep soils on south-facing slopes. *Bromus ciliatus* and *Agropyron trachycaulum* are other characteristic grasses. The most frequent forbs are *Achillea lanulosa, Potentilla pulcherrima, Linum lewisii, Erigeron speciosus, Thalictrum fendleri, Lathyrus leucanthus,* and *Vicia americana.*

In considering the floristic relationships of the communities in the area, it was arbitrarily decided to include only those species occurring with a frequency of 50 per cent or more since only these contribute significantly to the definition of homogeneity of the vegetational pattern. The floristic relationships of these species within the vegetational patterns are shown in Figure 3. Species with less frequency contribute only to minor diversities within the patterns.

Boreal, and Central and Northern Rocky Mountain elements are represented in all of the communities, although the latter plays only a minor role in each community. The boreal element occurs most prominently in the aspen community, where it plays the dominant role. Also species with distributions widespread in western North America contribute to all of the vegetational patterns, but they play the dominant role in the sage-

brush, fescue, and spruce-fir communities, being especially noteworthy in the sagebrush community where 63 per cent display this relationship. The Central Rocky Mountain element is represented in all but the fescue and sagebrush communities; it is the most conspicuous element in the upland herb community and takes second place in the alpine zone. The Central and Southern Rocky Mountain element is present in all communities except the alpine, and it places second in the upland herb, fescue, and aspen communities. Species widespread throughout the Rocky Mountains are represented in all but the upland herb community, but assume no outstanding role in any community.

Four other elements are represented only in a limited number of communities. The circumboreal element is restricted to the alpine, upland herb, and aspen communities, but dominates the alpine zone. Species with Great Basin-Colorado Plateau affinities are represented only in the sagebrush and alpine communities which are at elevational extremes. A similar situation in regard to the presence of desert elements in the alpine zone of the Sierra Nevada was noted by Went (1953). Species with Northern Rocky Mountain affinities and those widespread over North America play only insignificant roles in a few communities.

It should be pointed out that, despite the evident relationships of the flora (fig. 2) and the floristic relationships of those species which are at least 50 per cent frequent in the communities (fig. 3), the physiognomic expression of the communities is more similar to that in the adjacent mountainous areas in the Great Basin and Colorado Plateau than to that on the eastern slope of the Rockies. Also the *zonal sequence* appears to be in response to a gradient toward more extreme xeric conditions than in many other localities on the western slope of the Rockies and in adjacent areas in eastern Utah. These conclusions are borne out by the following features. A distinguishable assemblage of grasses and forbs, which occurs in the Crested Butte area between the alpine and spruce-fir zones, has not been recorded on the eastern slope of the Rockies. This upland herb zone does occur, however, in the Uinta Mountains (Graham, 1937) and the Wasatch Mountains (Ellison, 1954). The spruce-fir zone on both the eastern slope and in mountainous areas in the Great Basin usually occupies about a 2,000-foot altitudinal range, but here, except on north exposures, it is restricted to about 1,000 feet, and after fire is replaced more commonly by a grassland than by lodgepole pine or aspen forests. A forest dominated by *Pinus ponderosa* var. *scopulorum* and *Pseudotsuga taxifolia,* which is general on the eastern slope below the spruce-fir zone, is represented in this area only by scattered or isolated trees along canyon walls. This pine-Douglas fir zone is also absent over much of the western slope and adjacent areas in eastern Utah. A zone dominated by *Pinus ponderosa* var. *scopulorum,* but usually without *Pseudotsuga taxifolia* as an associate, does occur, however, in many places in the Great Basin. In place of the pine-Douglas fir zone, below the spruce-fir zone, there usually occurs an altitudinally-defined zone of aspen. Although aspens are abun-

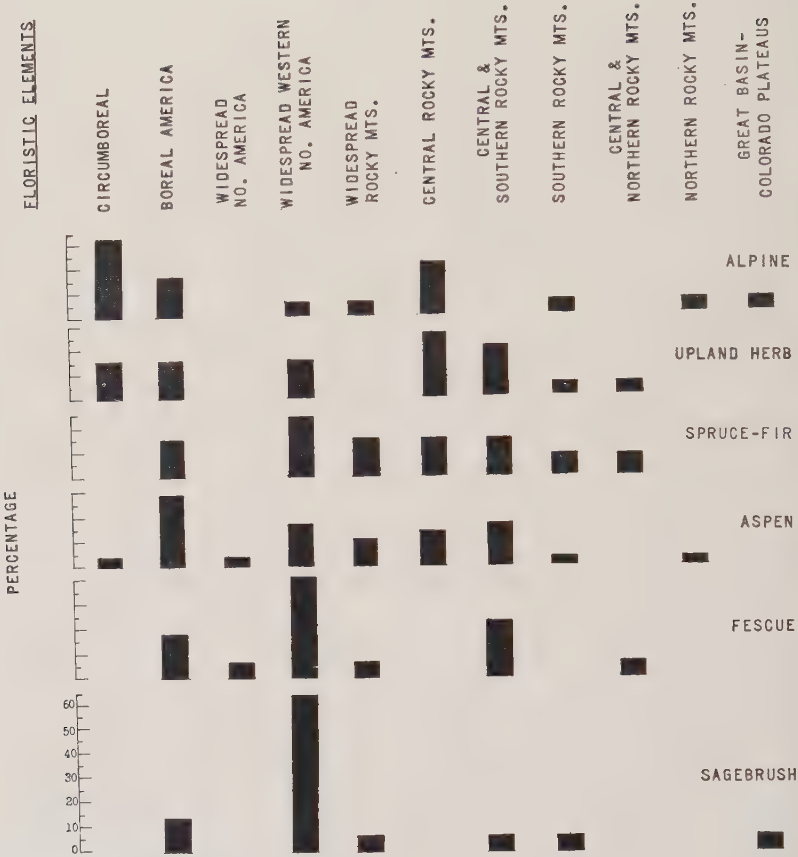


FIG. 3. Floristic relationships of species which are at least 50 per cent frequent within the principal communities in the Crested Butte area.

dant on the eastern slope, they usually do not form a well-defined belt such as has been reported for western Colorado and central Utah (Baker, 1925), the LaSal Mountains (Tanner and Hayward, 1934), the Uinta Mountains (Graham, 1937), the Wasatch Mountains (Lull and Ellison, 1950), and many other areas in the Great Basin. The interzonal grassland community dominated by *Festuca thurberi* also has been reported elsewhere only from the Abajo Mountains (Ellison, unpublished ms.). Generally, over many areas on the western slope of the Rockies and in the Great Basin, the next zone below the aspen belt is one dominated by oaks, followed by one dominated by pinyon and junipers. In the Crested Butte area these zones are absent and in their place is one dominated by *Artemisia tridentata*. Discussions by numerous authors concerning the zonal sequences and the presence or absence of ponderosa pine, oak, pinyon-juniper, and high-altitude sagebrush zones are correlated by Langenheim

(1953). The relatively unique zonal sequence in the area of the Crested Butte Quadrangle may result partially from a steep precipitation gradient between 8,000 and 10,000 feet and partially from the fact that 66 per cent of the area is southwest-facing.

Documentary Collections

Although specimens were collected throughout the area of the quadrangle, intensive collecting was done over the 100 square miles where the vegetation was mapped. Because field investigations of this type are dependent upon sampling procedures, it is improbable that the list is complete. Therefore species (marked with an asterisk) from nearby similar habitats outside the area are included. Eventually it is expected that they will be found within the area of the quadrangle. The list includes 579 species, 245 genera, and 64 families. Numbers following specific epithets are the collection numbers of the author.

Aceraceae

Acer glabrum Torrey, *68, 270*
*A. negundo L., *1430*

Anacardiaceae

*Rhus trilobata Nutt., *1328*

Apocynaceae

Apocynum androsaemifolium L., *500*

Asclepiadaceae

Asclepias hallii Gray, *476, 788*
A. speciosa Torrey, *1376*
*A. subverticillata (Gray) Vail, *1441*

Berberidaceae

Berberis repens Lindl., *184-48, 19*

Betulaceae

Alnus tenuifolia Nutt., *135-48, 1270*
Betula glandulosa Michx., *317-48, 27*
*B. occidentalis Hook., *135-48, 1379*

Boraginaceae

*Cynoglossum officinale L., *1377*
Cryptantha bakeri (Greene) Payson, *1209*
Eritrichium elongatum Wight, *444, 1014, 1274, 2109*
Hackelia floribunda (Lehm.) Johnst., *107, 434, 1420, 3944*
Lappula redowskii (Hornem.) Greene, *114, 1263*
Mertensia ciliata (James) G. Don, *105-48*
M. franciscana Heller, *3957*
M. fusiformis Greene, *10, 11, 1222*
M. viridis Nels. var. cana (Rydb.) Williams, *102-48, 4, 276, 341, 362, 396, 808, 1063, 1113, 1300*
Plagiobothrys scopulorum (Greene) Johnst., *1141*

Callitrichaceae

Callitriche palustris L., *444-48*

Campanulaceae

Campanula parryi Gray, *328, 376, 593, 3866*
C. rotundifolia L., *366, 593, 2145*
C. uniflora L., *439*

Capparidaceae

Cleome serrulata Pursh, *2016*

Caprifoliaceae

Linnaea borealis L., *142, 481, 3914*
Lonicera involucrata Banks ex Sprengel, *182-48, 38*
Sambucus racemosa L., *180-48, 31, 3904*
Symphoricarpos occidentalis Hook., *76*
S. tetonensis A. Nels., *121, 1325*
S. vaccinioides Rydb., *780, 1205, 1314, 1535, 3938*

Caryophyllaceae

Arenaria congesta Nutt., *98-48, 358, 795*
A. macrantha (Rydb.) Nels., *3968*
A. lateriflora L., *126*
A. obtusiloba (Rydb.) Fernald, *427, 2105*
A. sajanensis Willd., *70, 905, 1361, 2106*
A. verna L., *455*
Cerastium arvense L., *1225, 1521*
C. beeringianum Cham. & Schlecht., *560-48, 52, 814*
Lychnis apetala L., *901, 1461*
L. kingii Wats., *433*
Paronychia pulvinata Gray, *1288*
Silene acaulis L., *538-48*
S. menziesii Hook., *174, 822, 882*
S. scouleri Hook., *356, 416, 425*
Sagina saginoides (L.) Karst., *3844*
Stellaria longipes Goldie, *98, 739, 1278*
S. jamesiana Torrey, *1392*
S. umbellata Turcz., *526*

Celastraceae

Pachystima myrsinites Raf., *424-48, 544-48, 24*

CHENOPODIACEAE

Chenopodium album L., *1455*
C. fremontii S. Wats., *323 a*
Monolepis muttalliana (Schult.) Greene, *323 b*

COMPOSITAE

Achillea lanulosa Nutt., *515-48, 1112, 3879*
Agoseris aurantiaca (Hook.) Greene, *22, 161, 972*
A. glauca (Pursh) D. Dietr., *130, 494, 920, 972, 892, 1097, 3936*
Anaphalis margaritacea (L.) Benth. & Hook., *528*
Antennaria anaphaloides Rydb., *325*
A. concinna A. Nels., *350*
A. microphylla Rydb., *829, 1136*
A. parviflora Nutt., *87*
A. rosea Greene, *89-48, 59, 129*
Arnica cordifolia Hook., *46, 64, 90, 371, 1367, 1399, 3908*
A. fulgens Pursh, *493*
A. latifolia Bong., *400 a, 487*
A. mollis Hook., *3963*
A. parryi Gray, *584, 970, 1395, 3907*
A. rydbergii Greene, *1001, 2111*
Artemisia dracunculus L., *531-48, 214, 346, 3929, 3945*
A. frigida Willd., *90, 1531, 3863*
A. ludoviciana Nutt., *371, 825, 841, 3969*
A. scopulorum Gray, *215-48, 820, 1047*
A. spithamaea Pursh, *390*
A. tridentata Nutt., *572, 3864, 3928*
Aster bigelovii Gray, *3868, 3930*
A. coloradensis Gray, *961*
A. engelmannii Gray, *1521, 3903*
A. foliaceus Lindl., *511, 1100, 3869, 3943*
A. foliaceus Lindl. var. frondosus Gray, *1083*
A. glaucodes Blake, *450*
A. leucanthemifolius Greene, *507*
A. porteri Gray, *1261*
Bahia dissecta (Gray) Britton, *466*
Brickellia grandiflora (Hook.) Nutt., *1433*
Chaenactis alpina (Gray) Jones, *331, 585, 1504, 3889, 3897, 3954, 3972*
C. douglasii (Hook.) H. & A., *113, 386, 1333*
Chrysopsis hispida (Hook.) DC., *464, 3920*
C. villosa (Pursh) Nutt., *218, 220, 400 a, 570, 1011, 3947*
Chrysothamnus parryi (Gray) Greene, *555, 594, 1121, 1128, 3856*
C. viscidiflorus (Hook.) Nutt., *374, 1122, 1127, 3857*
Cirsium drummondii T. & G. var. acaulescens (Gray) Macbride, *1130*
C. eatonii (Gray) Robins., *3887*
C. parryi (Gray) Petrak, *3885*
C. scopulorum (Greene) Cockl., *921, 1129, 3896, 3962*
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P. tremuloides Michx., *1537*
Salix anglorum Chamisso var. antiplasta Schneider, *547-48, 101, 108, 110, 111, 410, 447 b, 818, 1094*
S. barclayi Andersson, *341-48, 376-48, 41, 93, 102, 106, 107, 118, 133, 894*
S. barclayi Andersson var. hebecarpa Andersson, *120-48*
S. brachycarpa Nutt., *373-48, 376-48, 105, 109, 245, 411, 486, 581, 716*
S. cascadensis Cockl., *985*
S. drummondiana Barratt var. subcoerulea (Piper) Ball, *28, 84, 715*
S. irrorata Andersson, *700*
S. melanopsis Nutt., *732*
S. nivalis Hook., *447 a*
S. nivalis Hook. var. saximontanus (Rydb.) Schneider, *103-48, 307, 597*
S. planifolia Pursh var. monica (Bebb) Schneider, *104-48*
S. pseudocordata (Andersson) Rydb. var. aequalis Andersson *707, 731, 733*
S. pseudolapponum Von Seeman, *549-48, 48, 112, 117, 298, 308, 342, 807, 940, 1093*
S. scouleriana Barratt, *253, 717*
S. scouleriana Barratt var. coetanea Ball, *119, 715*
S. wolfii Bebb, *114, 115, 116, 318*

SAXIFRAGACEAE

Heuchera parvifolia Nutt. var. flavescens R. B. & L., *194, 1274*
Lithophragma bulbifera Rydb., *1232*
Mitella pentandra Hook., *835, 1004*
M. stauropetala Piper var. stenopetala (Piper) Rosend., *164, 769*
Parnassia fimbriata Banks, *598-48*
Saxifraga arguta Don, *600-48, 259, 502*
S. bronchialis L., *601-48, 360*
S. caespitosa L. subsp. exaratoides (Simon) Engl. & Irmsh., *430, 1464, 2101*
S. cernua L., *804, 1470*
S. columbiana Howell, *1091*
S. chrysantha Engelm., *1460*
S. debilis Engelm., *499, 881*
S. flagellaris Willd. var. platysepala Traut., *435, 803, 1459*
S. oregana Howell, *259, 311, 1091*
S. rhomboidea Greene, *546-48, 599-48, 602-48, 289, 424*
Sullivantia purpusii (Brand) Rosend., *1020*

SCROPHULARIACEAE

Besseya alpina (Gray) Rydb., *438, 2104*
Castilleja chromosa A. Nels., *708, 1210, 2011*
C. linariaefolia Benth., *219, 3932*
C. occidentalis Torrey, *1079, 2057, 3958*
C. rhexifolia Rydb., *394-48, 3959*
C. septentrionalis Lindl., *495-48, 235*
Chionophila jamesii Benth., *436, 809, 1469*
Mimulus guttatus DC., *406-48, 582*
Orthocarpus luteus Nutt., *357*
Pedicularis crenulata Benth., *411-48, 68*
P. groenlandica Retz., *398-48, 572-48, 557*
P. parryi Gray, *565, 2147*
P. paysoniana Pennell, *204, 249, 973*
P. procera Gray, *355, 1416*
P. racemosa Dougl., *244, 2150*
P. scopulorum Gray, *69, 815*
Penstemon barbatus (Cav.) Roth. subsp. torreyi (Benth.) Keck, *492-48*
P. caespitosus Nutt., *83*
P. crandallii A. Nels., *774*
P. harbourii Gray, *412-48, 942, 2152, 3900*
P. humilis (Nutt.) Gray, *575-48*
P. rydbergii A. Nels., *498-48, 196, 1332*
P. strictus Benth., *132, 339*
P. teucrioides Greene, *1298*
P. whippleanus Gray, *420-48, 248, 490, 1391*
Veronica alpina L., *405-48, 40, 2149*
V. americana Schwein., *80, 790, 2000*
V. serpyllifolia L., *3845*

SELAGINELLACEAE

Selaginella densa Rydb., *56, 3967, 3988*

SPARGANIACEAE

Sparganium angustifolium Michx., *454-48*

UMBELLIFERAE

Angelica ampla. Nels., *3841, 3892*
A. grayi C. & R., *418-48, 919, 2158*
Conioselinum scopulorum (Gray) C. & R., *1026, 3906*
Heracleum lanatum Michx., *504-48, 505-48, 377*
Ligusticum porteri C. & R., *503-48, 200, 216, 994, 3905, 3934*
Lomatium dissectum (Nutt. ex Torr. & Gray) Mathias & Constance, *2142*
L. simplex (Nutt.) F. Macbr., *712, 771, 1274*
Oreoxis alpina (Gray) C. & R., *252, 440, 710, 2036*
Osmorhiza obtusa (C. & R.) Fern., *789, 954, 1398*

O. occidentalis (Nutt.) Torrey, *217, 3901*
Oxypolis fendleri (Gray) Heller, *419-48, 94, 228, 530, 1092*
Pseudocymopterus montanus (Gray) C. & R., *422-48, 519-48, 564-48, 6, 114, 385, 711, 723*

Urticaceae

Urtica gracilis Ait., *201*

Valerianaceae

Valeriana capitata Pall. subsp. acutiloba (Rydb.) F. G. Meyer, *5, 300, 404, 1050*
V. edulis Nutt. ex. T. & G., *1040, 1364, 1421*

Violaceae

Viola adunca Sm., *540-48, 585-48, 590-48, 592-48, 2, 53, 58, 286, 567, 1241*
V. adunca Sm. subsp. ashtonae Baker, *212-48, 597-48*
V. canadensis L., *595-48, 26*
V. nuttallii Pursh, *586-48, 488-48, 591-48, 593-48, 12, 1221*
V. palustris L., *1425*
V. rugulosa Greene, *587-48, 589-48, 594-48*

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Literature Cited

Baker, C. F. 1898. Botanizing in the La Plata Mountains. Plant World 2:29–32.

Baker, F. S. 1925. Aspen in the Central Rocky Mountain region. U.S. Dept. Agric. Bull. 1241:1–46.

Brandegee, T. S. 1876. The flora of southwestern Colorado. Bull. U.S. Geol. and Geog. Survey Terr. 2:227–248.

Cary, M. 1911. A biological survey of Colorado. No. Am. Fauna 33. 256 pp.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecol. Monog. 24:89–184.

———. Festuca thurberi grassland. Indian Creek, Albajo Mts., Utah. Unpublished data in files of Intermountain Forest and Range Experiment Station, U.S. Forest Service, Ogden, Utah.

Graham, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. Ann. Carnegie Mus. 26. 432 pp.

Langenheim, J. H. 1953. The plant communities and their environment in the Crested Butte area, Gunnison County, Colorado. Ph.D. thesis (unpublished), Univ. Minnesota.

Lull, H. and L. Ellison. 1950. Precipitation in relation to altitude in Central Utah. Ecology 30:479–484.

Porter, T. C. and J. M. Coulter. 1874. Synopsis of the flora of Colorado. U.S. Geol. and Geog. Survey Terr. Misc. Publ. 4. 180 pp.

Robbins, W. W. 1910. Climatology and vegetation in Colorado. Bot. Gaz. 49:256–280.

Schmoll, H. M. 1935. Vegetation of the Chimney Rock area, Pagosa-Piedra region, Colorado. Private edition, distributed by Univ. of Chicago Libraries, Chicago, Ill.

Tanner, V. M. and C. L. Hayward. 1934. A biological survey of the LaSal Mts., Utah. Utah Acad. Sci. 11:209–235.

United States Dept. Agriculture Yearbook. 1941. Climate and Man: 798–808.

United States Dept. Commerce. 1952. Climatological Data, Annual Summary, Colorado 57:172–181.

Went, F. W. 1953. Annual plants at high altitudes. Madroño 12:109–114.

REVIEWS

Manual of the Plants of Colorado. By H. D. Harrington. x + 666 pp., Sage Books, Denver. $8.00.

The identification of plants in much of the Rocky Mountain area has been greatly hampered for many years by the lack of up-to-date manuals. The two manuals which have been of most value for Colorado, namely, Coulter and Nelson's "New Manual

of Rocky Mountain Botany" (1909) and Rydberg's "Flora of the Rocky Mountains and adjacent plains" (1917) are not only out of print but are considerably outdated in their nomenclature and taxonomy. A reflection of the need for an up-to-date treatment may be gained from a statement in the introduction of the present work that "about one out of every 30 species listed here constitutes a new record for the state or at least is not credited to Colorado in the monographs and manuals."

Dr. Harrington, Associate Professor of Botany and Curator of the Herbarium at Colorado A. & M. College, Fort Collins, has prepared analytical keys and complete descriptions for the identification of 2,794 species and 351 infraspecific taxa of ferns and flowering plants in the state. He has incorporated about 350 entities in the text for which he has seen no actual specimens from the state, but which are plants actually reported for Colorado or listed from adjacent areas and to be expected within the state. However, the source of these reported occurrences is not indicated.

Following the introduction there is a discussion of the vegetation zones in Colorado contributed by David F. Costello, Range Conservationist of the United States Forest Service. This provides a general topographic and floristic analysis of the vegetation with the characteristic taxa of the various vegetation types enumerated. A key to the families precedes the main taxonomic treatment and a complete glossary and index to common names and genera concludes the volume.

In the taxonomic treatment proper, which forms the bulk of the manual, established common names are employed (but none are coined) for families and genera. No common names, however, are given for species. Infraspecific taxa are cited as straight trinomials with their rank indicated in parentheses following the name. The place of publication for each species is given. The book has been printed by photo-offset from typescript and the small type (especially in the keys) is not easily read. Oftentimes, the impression is unevenly reproduced so that there are lighter or darker sections on the same page. Alignment of the right hand margins of the typescript would have improved the appearance of the finished text and would also have effected an economy with respect to the number of pages.

Dr. Harrington has maintained a fairly conservative viewpoint in his delimitation of taxa and much of the work is in accord with current treatments. He has wisely drawn upon the assistance of specialists for the accounts of some genera, either in whole or in part: *Scirpus* by Alan Beetle, *Juncus* by F. J. Hermann, *Salix* by E. C. Smith, *Oxytropis* and *Astragalus* by C. L. Porter, *Penstemon* by C. Wm. T. Penland, *Hymenoxys* by K. F. Parker, and *Balsamorhiza, Wyethia* and *Helianthella* by W. A. Weber. Likewise, contemporary taxonomic papers have been closely followed in the preparation of many other groups. The manual appears to be a careful compilation of existing knowledge regarding the Colorado flora, and notes of critical value, while limited, are scattered throughout the text. The distributions given for the various species are based on specimens actually studied and these seem to have been principally specimens in the herbaria of the Colorado-Wyoming area. Valuable collections of Colorado plants in some of the larger herbaria of the United States appear not to have been consulted. The reviewer has noted some Colorado collections cited in taxonomic papers from these larger herbaria which either extend the range of the species or establish an otherwise doubtful record for the state and which are not accounted for in the present manual. Although altitudinal ranges are given for most species, an arbitrary device is employed which divides the state into nine equiformal areas for describing the range of each species.

The ponderous size (8½″ × 11″ and 2″ thick) scarcely makes the book a "manual" that can be used with ease in the field. The technical approach and the lack of illustrations, as well as the cost, may deter the lay student or interested amateur from using the book. Nevertheless, the manual represents a milestone in Colorado botany which should prove of much help to the professional taxonomist. It is to be hoped that it will provide a stimulus and a working foundation for much needed studies of a highly interesting and rich flora.—G. Thomas Robbins, Department of Botany, University of California, Berkeley.

The Polyporaceae of the United States, Alaska and Canada. By LEE ORAS OVERHOLTS. Prepared for publication by Josiah L. Lowe. University of Michigan Scientific Series, Volume XIX. xiv + 466 pp., 132 pls. 1953. University of Michigan Press, Ann Arbor. $7.50.

Mycologists, plant pathologists and others have long awaited the appearance of this work as Dr. Overholts was the leading specialist in the Polyporaceae in America for many years. It is the first unified comprehensive treatment of this family for the area.

The first draft of the manuscript was written in 1933, but publication facilities were not secured at that time. Dr. Overholts made corrections and additions for new material as his health would allow until the time of his death in 1946. It is especially fortunate that Dr. Josiah L. Lowe, a widely known and able specialist in this field was willing to complete the work necessary for publication of the manual. He has included new material in the keys, text, and illustrations and has brought the whole to a well-finished product.

The introduction gives a summary of the history of classifications of the family, and of the variations in generic concepts held by different students of these fungi. An explanation is given of the morphological characters and terminology employed. Also the biology and the role of these fungi in nature is discussed.

The taxonomic treatment is the conservative one that characterized Dr. Overholts' earlier publications. The key to genera limits the family to ten old, long established genera. Two of these, the non-pileate genera *Merulius* and *Poria*, are not treated in this manual.

This treatment is in striking contrast to those of several other workers who have segregated a large number of other genera within the family. The author defends his position in this matter in his introductory chapter. The more recent publications of Donk (1933), Pilat (1936-1942), Cunningham (1946-1948), and Pinto-Lopes (1952) employ quite different criteria as their basis of classification. The first two are cited, but none of them is reviewed, since they appeared after the manuscript was written.

The keys to species are well constructed and simple. A conservative synonomy for each species is provided. Clear concise technical descriptions, using both macroscopic and microscopic characters, are given for each species as well as habitat, distribution and published illustrations. Two hundred thirty-five species and twelve varieties are so treated.

An outstanding feature of this manual is the abundant and excellent illustrations consisting of 675 half-tone illustrations and more than 200 line drawings. The half-tones, although necessarily reduced in size, are clear and furnish information as to macroscopic characters, while the line drawings illustrate the character of the hymenium and spores.

The citation of publication data for each species, the synonyms listed, and the bibliography of 238 titles provide excellent references to the literature of the field. A glossary furnishes an explanation of the terminology used.

This manual will be a valuable standard work for many years to come, and the editor and publishers are to be congratulated on the quality of the publication.—LEE BONAR, Department of Botany, University of California, Berkeley.

NOTES AND NEWS

Authors of scholarly works which may be of great importance to a particular field and yet, because of their probable limited sale, may be too expensive for publication in the United States, will be interested to learn of the organization of the International Scholars Forum. The Advisory Board of the Forum has arranged to receive and appraise for publication by a European press such manuscripts as may be submitted to them by American authors. Details of the plan may be obtained from the Librarian of the Honnold Library, Claremont, California.